

Waldrand und damit auch näher an den umliegenden landwirtschaftlich genutzten Flächen als die Zufallspunkte. Diese Baue gewährleisteten den Dachsen das ganze Jahr über Zugang zu einem optimalen Nahrungsangebot, sei es in den vielfältigen Mischwaldbeständen innerhalb des Waldes oder sei es auf den landwirtschaftlich genutzten Äckern und Wiesen außerhalb des Waldes. Die Dachse können so ihre Nahrungssuche den saisonalen Veränderungen im Nahrungsangebot optimal anpassen. Baue wurden meistens in Flächen mit wenig Bodenbedeckung und weiter als 50 Meter vom nächsten Weg entfernt gefunden. Nadelwaldbestände wurden gemieden. Einzelstehende, alte Fichten (*Picea abies*) in Laubwaldbeständen jedoch wurden oft als Standorte für Baue mit ein bis zwei Eingängen genutzt. Ihr flaches Wurzelwerk erleichtert das Graben und verhindert das Einstürzen des Baues. Ein hoher Deckungsgrad der Vegetation und damit ein guter Sichtschutz spielte eine wichtige Rolle für die Auswahl der Baustandorte. Sichtschutz kann jedoch auch durch andere Faktoren, wie Topographie und Entfernung zum nächsten Weg, gewährleistet werden. Insbesondere die kleinräumig diverse Topographie um die Baue scheint ein bisher wenig beachteter Schlüsselfaktor für die Anlage eines Baues zu sein. Die Ergebnisse dieser Studie sprechen dafür, dass ein großes Laubwaldgebiet mit einer stark ausgeprägten Topographie ein sehr gutes Dachshabitat darstellt.

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Authors' addresses:

TATJANA C. GOOD, Department of Ecology and Evolutionary Biology, Princeton University, Princeton, NJ 08544-1003, USA; KARIN HINDENLANG, Swiss Federal Institute for Forest, Snow and Landscape Research (WSL), Zürcherstrasse 111, CH-8903 Birmensdorf, Switzerland; STEPHAN IMFELD, Spatial Data Handling Division, Geographical Institute, University of Zurich-Irchel, Winterthurerstrasse 190, CH-8057 Zurich, Switzerland; BERNHARD NIEVERGELT, Wildlife Research and Conservation Biology, Zoological Institute, University of Zurich-Irchel, Winterthurerstrasse 190, CH-8057 Zurich, Switzerland.



Original investigation

Age and sex distributions in the catches of belugas, *Delphinapterus leucas*, in West Greenland and in western Russia

By M. P. HEIDE-JØRGENSEN and CHRISTINA LOCKYER

Greenland Institute of Natural Resources, Nuuk, Greenland and Danish Institute for Fisheries Research, Charlottenlund, Denmark

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Abstract

Age and sex were determined for belugas or white whales, *Delphinapterus leucas*, harvested in West Greenland in 1985–86 and 1989–1997. There was a clear segregation of whales in the drive fishery conducted during autumn in Qaanaaq and Upernavik. Primarily immature whales of both sexes together with mature females were taken. Age was estimated from Growth Layer Groups (GLGs) in sectioned teeth, assuming the currently accepted criteria of 2 GLGs forming annually. The mean and median ages were increasing slightly in both sexes from Upernavik from 1985 through 1994. Both immature and mature whales were taken on the wintering grounds from Disko Bay and south. Estimation of survival was confounded by the large number of whales where only a minimum age could be assigned because of tooth wear at the crown (i. e. no neonatal line in the dentine). The apparent survival rates for belugas from West Greenland were estimated as 0.81 and 0.79 for females and males, respectively. Correction of these estimates for an observed population decline of 4.7% per year revealed true survival rates of 0.85 and 0.82 for females and males, respectively. The estimates of true survival rates are less than those determined for beluga populations in the White and Kara seas and in Alaska for comparable age truncations. Since the exploitation levels are much lower in these areas the low apparent survival rate from West Greenland strongly supports the evidence of a population decline. Colour change from grey to white occurs at mean ages of 8.5 yr and 9.1 yr and median lengths of 367 cm and 445 cm in females and males, respectively.

Key words: *Delphinapterus leucas*, age structure, Greenland, Russian Arctic

Introduction

Large numbers of belugas (white whales), *Delphinapterus leucas*, have been taken in commercial fisheries and Inuit harvests throughout the Arctic during the last 100 years. In Greenland the accumulated catches of belugas in this century amounts to more than 50 000 whales (HEIDE-JØRGENSEN 1994).

Despite the availability of samples very little is known about the sex and age frequencies in different harvesting situations; let alone survival rates calculated from catch-at-age data.

The belugas that are harvested along West Greenland are believed to be part of the

stock(s) of belugas that summer in the Canadian High Arctic (HEIDE-JØRGENSEN 1994). This stock is supposed to winter in West Greenland south of Disko Bay and aerial surveys of the population densities of belugas on these wintering grounds have indicated a substantial decline between 1982 and 1994 (HEIDE-JØRGENSEN and REEVES 1996). The most likely explanation for this apparent population reduction is that the large level of exploitation during the 1980s has exceeded the replacement yield of the stock. With this background it was considered important to further evaluate the status of the stock.

SERGEANT (1973) provided the first age frequencies from catches of belugas in Hudson Bay and while he realised the detrimental impact of tooth wear on age estimations he was able to show that maximum longevity was at least 25 yr for both sexes, under the assumption of deposition of two Growth Layer Groups (GLGs) per annum. BURNS and SEAMAN (1986) provided age frequencies from Alaska with a maximum life span of 38 yr but did not present details on the distribution for males and females. DOIDGE (1990) showed from age frequencies obtained in Northern Quebec that belugas have a maximum longevity of at least 31 and 33 yr for males and females, respectively. By use of a smoothing technique of the age frequencies from teeth without wear DOIDGE (1990) estimated annual survivorships for both sexes combined ranging from 0.69 to 0.93 for whales between 0 and 9 yr of age and between 0.94 and 0.97 for whales between 10 and 37 yr of age. Survivorship estimates for worn and unworn teeth lumped together were slightly lower for all age classes. The survival rates were slightly higher in Northern Quebec compared to Alaska especially after age 12 yr, but both studies were evidently violating the assumptions of both equilibrium of the population prior to sampling and representativeness of samples for the population age frequencies.

This study examines the changes in the age- and sex selectivity of the harvesting of belugas in West Greenland. The survival rates calculated for West Greenland belugas are

compared to survival rates from belugas in the White and Kara seas.

Material and methods

Age frequencies from West Greenland

Lower jaws were collected from the catches of belugas in West Greenland (Fig. 1). The jaws were registered and stored at freeze houses and kept frozen before and during shipment to the laboratory in Copenhagen. Teeth were extracted and stored frozen until sections were prepared according to methods described in HEIDE-JØRGENSEN, et al. (1994). Two trained readers independently counted the number of Growth Layer Groups (GLGs – see PERRIN and MYRICK (1980) for definition of GLG) in the teeth and age was determined as the mean of the two readings. 'Minimum age' refers to those teeth where an unknown number of GLGs were missing due to wear of the crown of the tooth. 'Complete age' refers to those teeth in which all GLGs, including the neonatal line, could be counted. Two GLGs were assumed to be deposited annually (HEIDE-JØRGENSEN et al. 1994). The same two persons made all the readings of GLGs except for the samples from 1993–94 where another trained reader replaced one of them. If the discrepancy between the two readers exceeded 3 GLGs the tooth was checked again by one of the readers and if the discrepancy was maintained, the age estimate would either be discarded or another tooth was prepared. Sex was determined by DNA analysis of skin samples extracted from the lower jaws (PALSBØLL et al. 1992).

The samples collected were stratified with regard to sex, area, and year. For each area and year, the mean, its standard deviation and the median of ages were calculated for both sexes. This was done separately for samples restricted to whales with minimum age and to whales with complete age.

Colouration of skin was classified to three groups; brown or brownish-grey, grey and white, for a subsample of 147 females and 119 male belugas that were examined before being flensed. Classification of skin colouration from the skin remains on the samples of lower jaws alone proved to be unreliable, whereas all the whales with length measurements had been examined by the first author before they were flensed. For the change in colouration from grey to white colouration mean age and associated variance was determined by use of the method of DEMASTER (1978) after smoothing of a curve fitted to the data.

Age frequencies from the White and Kara seas

Age frequency data from the beluga harvest in the White and Kara seas was compared with the age distribution from West Greenland. A sample of 570 whales was collected from the commercial

hunt in the White and Kara seas in the 1970s and early 1980s (see OGNETOV 1981 for a description of a subset of the sample).

The growth of belugas in the White and Kara seas resembles the West Greenland belugas more than any other beluga population (HEIDE-JØRGENSEN



Fig. 1. Map of municipalities and areas in West Greenland mentioned in the text.

and TEILMANN 1994) although their tooth wear begins at a much later age (HEIDE-JØRGENSEN et al. 1994).

Estimation of survival rates

Apparent survival rates (i.e. survival rates uncorrected for population changes) were estimated for the age frequencies from West Greenland and the White and Kara seas according to the method of ROBSON and CHAPMAN (1961). Because of underrepresentation of the youngest age classes in all samples, all age frequencies were re-coded from the modal age class upwards. Apparent survival rates were also calculated by fitting a negative exponential curve where the natural logarithm of the exponent is equivalent to the annual survival rate.

Statistical analysis

Data management and comparisons of means were conducted in Statview for Windows (version 5.0) and non parametric tests and non linear regressions were carried out in S-Plus (ver-

sion 4.5). Unless otherwise stated, significance was always determined at the 5% level.

Results

Selectivity in the beluga harvest in West Greenland

All sex and age classes of belugas are subject to harvesting in West Greenland (Fig. 2). Sampling during ten years between 1985 and 1997 resulted in an overall mean age of 7.7 yr in females and 6.5 yr in males of the harvested population older than 1 year in all municipalities and minimum and complete ages combined. In the samples more females than males were taken (712 vs. 596), but there was an equal proportion of both sexes among calves less than 1 year of age in Greenland (44 females, $n = 89$).

The limited number of samples from the municipality of Qaanaaq (formerly called

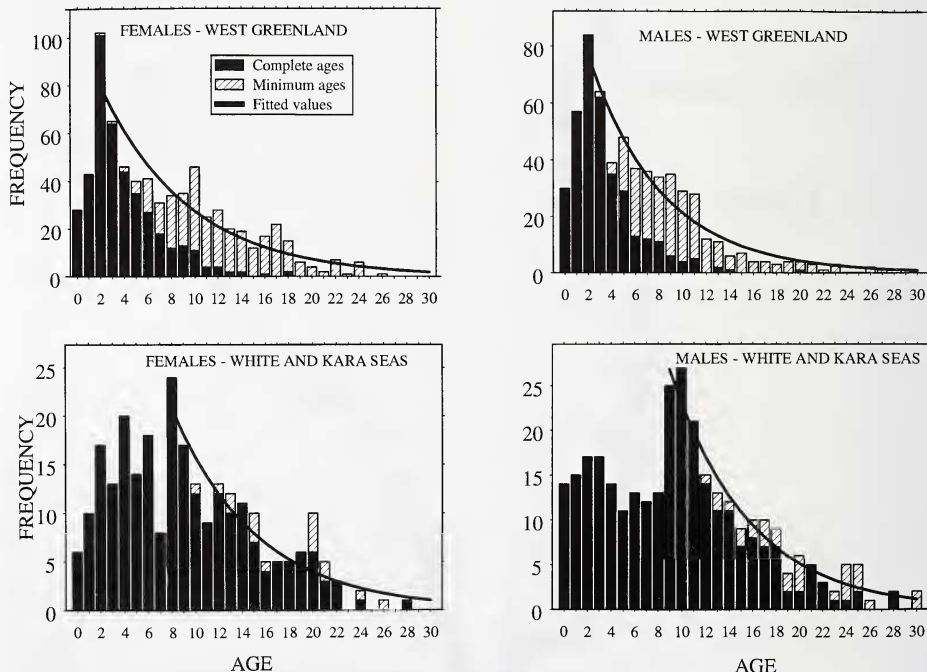


Fig. 2. Age-frequency distributions of male and female belugas from West Greenland and the White and Kara seas. Frequencies of complete and minimum ages are shown together with the negative exponential fit ($F = a \cdot \exp(b \cdot \text{AGE})$) from the modal age class. See table 2 for values of parameters from fitted functions.

Avanersuaq, see Fig. 1) collected in September 1993 showed that the catch primarily consisted of young animals (Tab. 1). The mean age of the samples from the municipality of Upernavik collected in late September and early October 1985 through 1994 or in 1993 alone were not significantly different from those collected in Qaanaaq (ANOVA, $p > 0.2$). The samples of whales taken in Uummannaq in the autumns of 1993 through 1996 indicated similar age structure as in Qaanaaq and Upernavik. Mainly young whales were taken in all three areas.

When contrasting the age and sex frequencies obtained from the autumn drive fisheries in Qaanaaq, Upernavik and Uummannaq, with that from the ice edge and open water hunt in Disko Bay and south, it is obvious that older whales are taken in Disko Bay (Tab. 1). This was evident both from comparisons of mean ages from all whales (older than 1 year) and from those with complete ages (t-test). Also, the samples collected from winter and spring catches in Disko Bay showed that less than 30% of the whales could be aged without bias (complete age) in contrast to Upernavik and Qaanaaq where more than 60% had complete age (Tab. 1).

Trends in mean age in the catches

Linear regressions of mean age on time showed that there was a significant increase in the mean age of harvested female and male belugas for which minimum age had been determined from 1985 through 1994 from Upernavik (ANOVA). The increase was also evident when groups where minimum and complete age had been determined were combined but could not be confirmed for females when complete age was considered alone. For the area from Disko Bay and south no significant trends in mean age could be detected between 1990 and 1997 for minimum age or minimum and complete ages combined. However, a significant increase was observed using complete age data for males but not for females ($p = 0.0588$). Since the minimum ages tend

to be truncated at the age when the neonatal is worn away this category of teeth is less reliable for detecting an increase in the mean age of catches. Thus the category with complete ages should be given more weight, which implies that there is a tendency for older males being harvested in both Upernavik and Disko Bay since the mid 1980s.

Comparison with age distribution in the White and Kara seas

The observed potential minimum life span of 30 yr in belugas from West Greenland was similar to what was found in the sample from the harvest in the White and Kara seas. This was, however, the only common feature of the two age distributions (see Fig. 2). Whereas immature belugas constituted the largest number of samples in West Greenland, mature whales of more than 7 yr constituted the majority of the samples from the White and Kara seas, where the mean ages also deviate significantly from West Greenland (Tab. 1). Because of the late onset of tooth wear in the belugas from the White and Kara seas less than 16% of the teeth had lost their neonatal line.

Survival rates of belugas

As tooth wear increases with age individuals with incomplete (minimum) age estimates are much more frequent in older age classes. Thus the apparent survival rates were generally much higher when individuals with minimum ages were included. Moreover, inclusion of minimum age estimates still leads to an underestimate of survival rates because the minimum age estimations underestimate the true age of the whales.

No significant differences were detected for apparent survival rates (age > 9 , t-test) or frequency distributions of all age samples from north and south of Disko Bay (Kolmogorov-Smirnov two sample test). Thus the two data sets were pooled.

The combined age distribution from West Greenland showed an underrepresentation of age classes 0 and 1 (Fig. 2), thus for the

Table 1. Mean ages of belugas older than 1 yr harvested in four different areas in West Greenland between 1985 and 1997 and in the White and Kara seas in the 1970s and 1980s. 'ALL' refers to both teeth with 'minimum' and 'complete' age

Years	1993				1985–1994				1993–1996				1986–1997				1970–1980			
	QAANAAQ		UPERNAVIK		Fermale		Males		Fermale		Males		Fermale		Males		Fermale		Males	
	All	Com- plete ages	All	Com- plete ages	All	Com- plete ages	All	Com- plete ages	All	Com- plete ages	All	Com- plete ages	All	Com- plete ages	All	Com- plete ages	All	Com- plete ages	All	Com- plete ages
Mean	6.2	4.8	6.0	3.7	6.0	4.1	5.3	3.6	8.2	2.8	6.6	6.3	10.4	6.0	8.4	5.1	9.4	8.9	10.1	9.0
SD	3.9	2.6	4.6	1.9	4.4	2.6	4.1	2.1	3.1	0.4	5.4	6.5	6.1	3.8	5.0	3.3	6.1	5.8	6.7	5.9
Median	5.5	4.0	5.0	3.5	4.5	3.5	3.5	3.0	9.0	2.8	5.5	3.5	10	5.5	8	5.0	9.0	8.0	10.0	10.0
N	41	31	27	17	364	258	283	209	11	2	13	8	283	79	253	67	258	242	312	282
Max age	16	10.5	23	8	22.5	18.5	26.5	13	11.5	3	20.5	20.5	26	18	29	14	28	28	30	28
% with com- plete age	76	63			71		74		20		62		28		27		94		90	

calculation of survival rates these age classes were excluded.

The age distributions from the White and Kara seas were radically different from what is seen in West Greenland. Whereas West Greenland age distribution peaks at 2 yr of age for both sexes the samples of belugas from the White and Kara seas were almost constant from age 0 to the peak at 8 yr in females and 10 yr in males (Fig. 2). Estimation of apparent survival rates for the White and Kara seas was thus conducted for the age frequencies older than 7 yr and 9 yr for females and males, respectively (Tab. 2).

The apparent survival estimates for the White and Kara seas were larger, albeit not significantly larger, than the estimates for West Greenland for similar truncations of the age classes (Tab. 2). However, significant difference (t-test) was only detected for the survival rate for male belugas estimated from the negative exponential model.

Change in colouration

Some beluga calves are born brown and others are grey, but usually the brown colouration changes at an earlier age (<5 yrs) and shorter length (<300 cm) than the grey colouration (Figs. 3 and 4). There is obviously a large overlap in the brown (or brownish-grey) and the grey classification which probably indicates difficulties in distinguishing between these two categories. The colour change from grey to white seems to be completed at a mean age of 8.5 yr for females (SD=0.6) and 9.1 yr for males (SD=0.5) and a median length of 367 cm and 445 cm for females and males, respectively (Figs. 3 and 4).

Discussion

Reliable calculation of survival rates for belugas taken in harvest operations depend on a variety of assumptions:

Table 2. Survival estimates for belugas from West Greenland and the White and Kara seas estimated by the method from ROBSON and CHAPMAN (1961) and by fitting a negative exponential curve (frequency = $a \cdot \exp(b \cdot \text{age})$). Only age classes older than 1 year of age are included in the estimations for West Greenland. For the White and Kara seas only age classes older than 7 yr for females and 9 yr for males, respectively, are included. 95% CI are shown in parenthesis

	SURVIVAL RATES	
	ROBSON and CHAPMAN	Negative exponential model
FEMALES – WEST GREENLAND		
Recoded ages from > 1 yr (n = 625)	0.86 (0.85–0.88)	0.88 (0.85–0.90)
Recoded ages from > 9 yr (n = 232)	0.81 (0.79–0.83)	0.84 (0.80–0.87)
MALES – WEST GREENLAND		
Recoded ages from > 1 yr (n = 500)	0.83 (0.82–0.85)	0.85 (0.83–0.87)
Recoded ages from > 9 yr (n = 123)	0.79 (0.75–0.82)	0.73 (0.69–0.78)
FEMALES – WHITE AND KARA SEAS		
Recoded ages from > 7 yr (n = 152)	0.84 (0.82–0.87)	0.87 (0.85–0.90)
MALES – WHITE AND KARA SEAS		
Recoded ages from > 9 yr (n = 161)	0.84 (0.81–0.86)	0.85 (0.83–0.87)

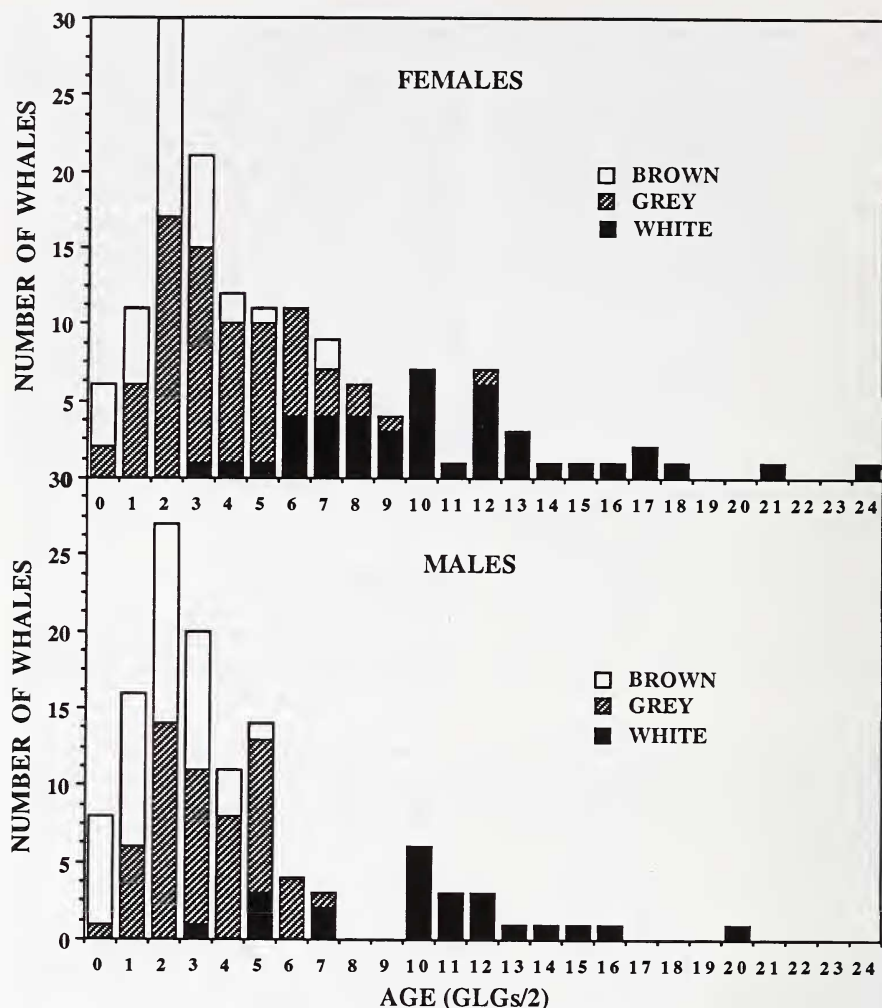


Fig. 3. Changes in colour phases in relation to age for female and male belugas from West Greenland.

1. Similar or identical methods for age estimation must be employed and preferably the techniques need validation from known age animals.
2. The samples collected from the harvest should be representative of the population and bias – if any – should be clearly discernible.
3. The survival need to be constant over time for the age groups involved in the estimation of survival and the population should be constant over the period when the age material was collected.

Age estimation technique

Identical methods for age estimation were used for all samples from Greenland and at least one person made readings of all teeth. Thus it seems reasonable to assume that the samples from Greenland are consistent with regard to age estimation and reading of GLGs. It is uncertain if the Russian samples are entirely comparable with those from Greenland. For validation of the age estimation method see HEIDE-JØRGENSEN et al. (1994).

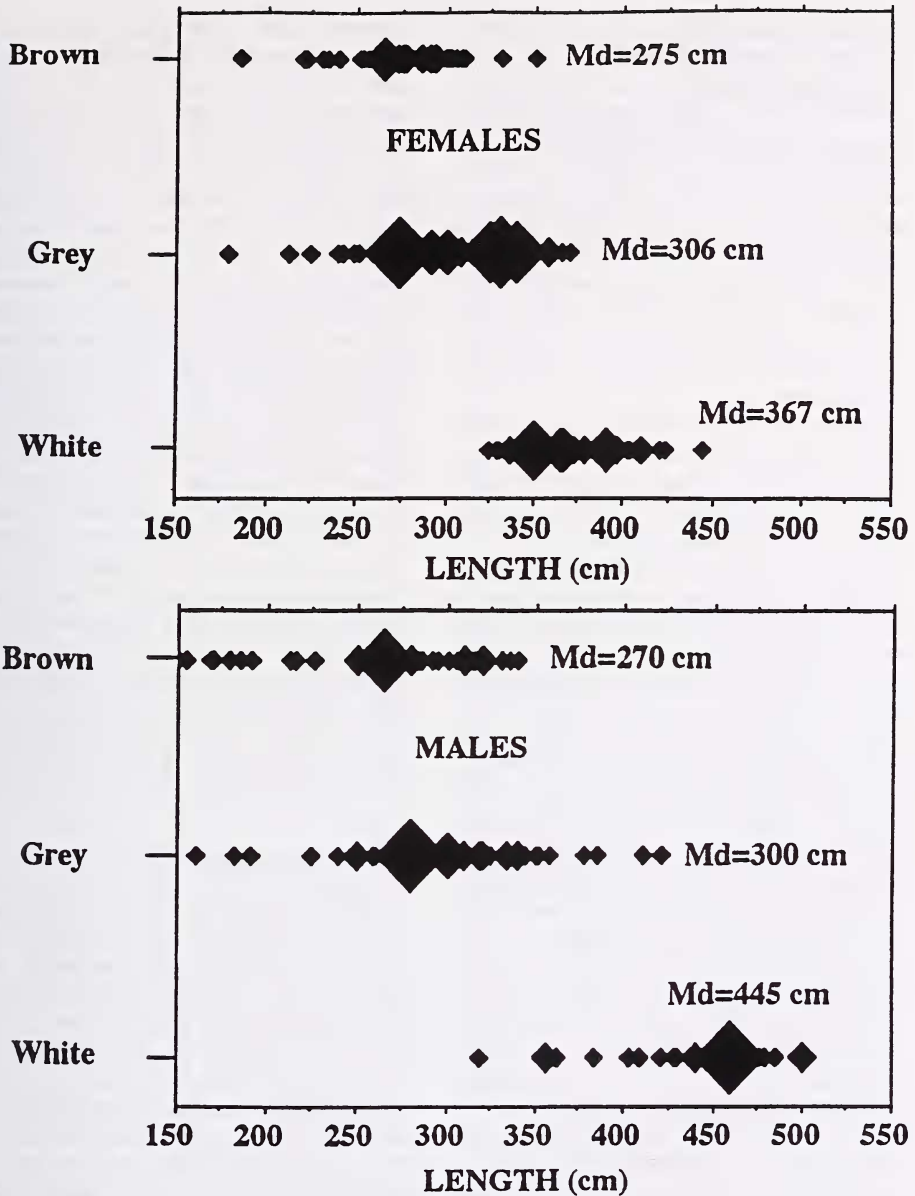


Fig. 4. Changes in colour phases in relation to length for female and male belugas from West Greenland. Md = median of cumulated numbers in each colour classification. Size of diamonds indicate the relative number of animals.

Bias in samplings

The samples collected for this study do not have an unbiased representation of the age and sex structure of the beluga population

as the selectivity varies with different hunting methods and seasons. The catches in Qaanaaq and Upernavik are taken in a drive fishery during a short period, usually the last week of September in Qaanaaq or

the first week of October in Upernavik. The catches usually consist of entire herds of belugas ranging in size from 20 to 250 whales. The catches can be considered as random samples of the segment of the beluga population that migrates south in a coastal corridor. There may be different composition of the herds encountered and there is probably some selectivity towards larger herds. However, the samples from the catch in Upernavik can at least be expected to reflect the annual composition of that particular fishery better than any of the other samples.

According to HEIDE-JØRGENSEN et al. (1994) mean age at tooth wear, i.e. when neonatal line disappears, for female and male belugas from West Greenland is 7.7 and 6.0 yr of age, respectively. For the samples from Upernavik this implies that less than 30% of the samples were from whales that exceed these ages. It also indicates that females are generally older for the Upernavik samples than the males, because they have a higher mean age but a similar proportion of 'minimum age' classifications. Age at sexual maturity in belugas from West Greenland is around 4–7 yr for females and 6–7 yr for males (HEIDE-JØRGENSEN and TEILMANN 1994). Thus few mature males were taken in Upernavik, whereas some mature females were included in the catches at least until 1992. In 1993 and 1994 an increasing proportion of mature animals of both sexes were taken. This fact and the apparent increase in mean age of whales taken in Upernavik may be a result of the intensive exploitation of the younger age segments of the population. The whales that were caught in 1993 and 1994 were taken around 1 October as in previous years, few whales were available to be driven and nothing suggested any decrease in hunting effort (HEIDE-JØRGENSEN own observations). The gradual shift to older segments of the population may be explained by a depletion of young whales that exceeded the recruitment to the population. The hypothesis of a general decline in the beluga population is supported by results from aerial surveys conducted at the wintering grounds between 1981 and 1994 (see HEIDE-JØRGENSEN and REEVES 1996).

The mean age of the whales taken in the autumn catches in Upernavik in 1993 was indistinguishable from the mean age of belugas taken in Qaanaaq earlier in the same season. Both samples were similar in their age distribution to samples collected at Grise Fjord presumably in the autumn (STEWART 1994). Because there were temporal differences in age classes taken in Upernavik, the selectivity in the harvest is likely due to different availability of certain age classes during the autumn migration.

The hunt in Disko Bay is conducted from powered boats in open water during November through January or from the ice edge in spring during March through May. Mature whales of both sexes have for several of the years been found on the wintering grounds around Disko Bay. Since the open-water and ice edge hunt in this area is characterised by catches of small herds (<10) of whales or single animals it may be considered to reflect the age structure of the population more randomly than the autumn drive fishery for large herds. This is because pods of mature males are often separated from mature females with young of both sexes.

Changes in population size

Estimation of survival rates is confounded by both selectivity in catches and a large proportion of whales with minimum ages which results in underestimates of maximum life span and survival. However, due to differences in tooth wear (HEIDE-JØRGENSEN et al. 1994) the sample from the White and Kara seas have less whales with incomplete age and probably reflect the true age more accurately. Apparent survival rates calculated for West Greenland including only females >7 yr and males >9 yr indicated survival rates that were lower albeit not significantly lower than those estimated for the White and Kara seas. Some of the difference between the two areas can be attributed to differences in tooth wear.

The largest catches of belugas in the White and Kara seas took place before 1966 when vessel hunting was stopped (OGNETOV pers.

comm.). During the period when the samples were obtained the beluga population in the White and Kara seas had been subject to some harvesting although exact statistics are not available. The Report of the International Whaling Commission (1982) list catch figures between 135 and 672 belugas per annum for 1976–1982 with years without catches in the White, Barents and Kara seas. Other researchers estimate that catches in this area during 1975–1980 remained below 1 200 whales (OGNETOV pers. comm.). In the 1980s catches have been dwindling (according to IWC reports from 1985 to 1991) and ceased after 1990 (OGNETOV pers. comm.). The reasons for the declining catches are more likely related to a reduced economical incentive for selling beluga products than to a reduced availability of the resource (STANISLAV BELIKOV pers. comm., OGNETOV pers. comm.). Recently it has been suggested that the beluga population in the western Russian Arctic is in a non-declining state and could potentially support a harvest of up to 530 belugas (OGNETOV pers. comm.).

During the 1980s catches have remained high in Greenland with an annual reported mean of 740 whales and there are no signs of a decline in hunting effort or in the economical incentives for the hunt (HEIDE-JØRGENSEN 1994). But aerial surveys of population densities on the wintering grounds in West Greenland indicate a linear decline of 4.7% (95% CI: 2.1–7.2) per year between 1981 and 1994 (HEIDE-JØRGENSEN and REEVES 1996). This population decline will severely affect the apparent survival rates calculated from the age material collected from the harvest. The apparent survival rates (q) can be converted into true annual survival rates (p) by $p = q/\lambda$, for the Robson and Chapman method and by $p = \exp(\ln q + (\lambda - 1))$ for the exponential model where λ , is the observed rate of population change. The true survival rates thereby become 0.85 and 0.83 for females and males, respectively, for the Robson and Chapman method applied to the belugas older than 9 yr in West Greenland. Similarly the true survival rates for the exponential model become

0.88 and 0.77 for females and males, respectively. These estimates are closer to the estimates derived from the age samples from the White and Kara seas.

In a study of harvested belugas in Alaska, BURNS and SEAMAN (1986) estimated age for 528 belugas collected between 1977–79 and 1980–83 and found several whales older than 30 yr and two as old as 38 yr. From the distribution of 332 males and females older than 5 yr they estimated a mean mortality rate of 0.094, equivalent to an annual survival of 0.91 for both sexes. This estimate was based on both minimum and complete age classifications and is therefore again an underestimate of true survivorship. The onset of tooth wear may occur a few years later in Alaska than in Greenland, but that is probably not the main explanation for the large and significant difference in survival in the two areas. The catches in Alaska have been reported to be between 241 and 345 belugas per year during 1980 to 1983 or an estimated 1.9% to 2.6% of the provisional population estimates and with no indications of a population decline over that period (LOWRY et al. 1989). Compared to the exploitation status in West Greenland it thus seems reasonable to assume that the apparent survival rates calculated for Alaskan belugas are less biased than estimates of survival in West Greenland. If the West Greenland age distribution is recalculated from age 5 yr (as for the Alaskan sample), females and males combined and corrected for population change with the negative exponential model, then the true annual survival rate becomes 0.9136, which is similar to the estimate from the far less exploited Alaskan population.

Changes in colour phase

Our estimates of change in colour phases are not entirely comparable to estimates from other studies, because several other researchers (e.g. BURNS and SEAMAN 1986) have used four colour phases rather than the three as chosen for this study. We found that using three colour phases was less sub-